A NEW RODENT GENUS (FAMILY HETEROMYIDAE) FROM THE TICK CANYON FORMATION OF CALIFORNIA

By WILLIAM G. REEDER

In 1940, R. H. Jahns discussed the statigraphy of the eastern Ventura Basin of southern California. In so doing, it was determined that the basal segment of the non-marine Mint Canyon section was distinct in fauna as well as lithology. The several lines of evidence which led to the segregation and description of the Tick Canyon formation were outlined in detail. In addition, as a result of faunal comparison, a late-early, or early-middle Miocene time of deposition was suggested for the Tick Canyon sediments.

This small fauna has been described as consisting of a single falconiform bird (Miohierax stocki Howard,) an oreodont (Merychyus calaminthus Jahns,) a leporid (Archaeolagus acaricolus Dawson,) and a single rodent which was listed as "Heteromyid, prob. n. gen. and sp." (Jahns 1940, p. 175). The latter had been examined by R. W. Wilson, who also furnished a descriptive statement enumerating several of the distinctive features of the form (op. cit. pp. 178, 182); the specimens were not figured. Through the courtesy of Dr. Theodore Downs, Los Angeles County Museum, these heteromyids were reexamined in connection with a larger problem. Their evident peculiarity, as seen after examination of all structurally-related forms (Reeder, 1956), warrants systematic recognition.

I am grateful to Mr. Ross A. Norris, staff artist of the Department of Zoology, University of Wisconsin, for preparation of the figures and plates.

FAMILY HETEROMYIDAE

Trogomys new genus

Type species: *Trogomys rupinimenthae* (described below). Distribution: Known only from the late Arikareean or early Hemingfordian Tick Canyon formation, Mint Canyon series of southern California.

Diagnosis: Molariform teeth brachydont and strongly rooted, with low cusps, as in *Perognathus*; true molars sexticuspidate; highly bilophodont, the cusps being conjoined to their apices, but with each cusp relatively low, rounded, and distinct, especially with slight wear; anterior cingulum present between

protoconid and protostylid; cingulum continues in unworn teeth as a minute remnant ridge on the anterobuccal margin of the metaconid; posterior cingulum present briefly at eruption between hypoconid and entoconid, at least of M_1 ; P_4 well developed, quadrate, quadricuspidate, but strongly bilophodont, with metalophid and hypolophid conjoining centrally; lower incisor slighty curvate and relatively narrow as in *Perognathus*, with anterior enamel surface curvate as seen in section; diastema short and concave throughout its length; least width of ramus at diastema about seven-eights occlusal width of M_1 ; masseteric crest terminates anteriorly behind, but slightly dorsal to mental foramen which arises on lateral surface of the disastema; I^1 is asulcate.

Etymology: Combined from trox, trogos, Gr., gnawer, and mys Gr., mouse.

Trogomys rupinimenthae, new species

Plate 39, fig. 1. Plates 40, 41.

Holotype: LACM (CIT) 5184, anterior fragment of cranium with full dental complement.

Hypodigm: (numbers are those of California Institute of Technology Collection, now at the Los Angeles County Museum.) The holotype: LACM (CIT) 5185, anteroventral fragment of cranium with right I¹, M²-M³ and left I¹, P⁴-M³; 5186, 5187, right partial rami with P₄-M₃; 5188, right partial ramus with I₁, P₄, M₃; 5189, left partial ramus with P₄-M₃; 5190, left ramus with I₁, P₄, M₂-M₃. All were collected from the Tick Canyon formation, Mint Canyon series, California Institute of Technology locality 201, "near the narrows of Vasquez Canyon, a tributary of Boquet Canyon, at a distance of approximately 10 miles by road (NE of) Saugus," Los Angeles County, California (Jahns, op. cit. p. 151).

Diagnosis: As for genus.

Etymology: Combined from *rupina*, L., rocky canyon and *mentha*, L., mint; intended to designate the stratigraphic series from which the specimens derived.

Description: The ramus is quite similar in conformation to that element of *Heliscomys* Cope and also *Cupidinimus* Wood (Plate 41). The anterior end of the ramus is slightly inflected at the diastema. The diastema is short and curvate throughout its length. Resembling *Cupidinimus* but not *Heliscomys*, the mental foramen opens into a marked depression one-third to one-half the length of the diastema anterior to P₄ and well down on the lateral face of the ramus. The masseteric crest rises in a gentle curve from the base of the ramus near the anterior border of M₂ and terminates anteriorly just behind and slightly dorsal to the

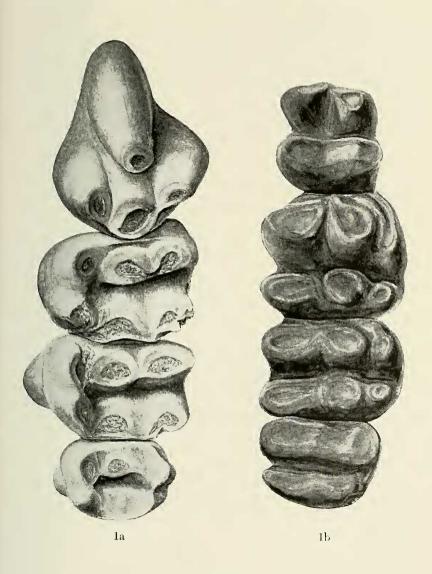


PLATE 39

Fig. 1a. *Trogomys rupinimenthae* new genus and species; holotype, LACM (CIT) 5184, left maxillary tooth row.

Fig. 1b. $Trogomys\ rupinimenthae$ new genus and species; referred specimen LACM (CIT) 5186, right mandibular tooth row.

mental foramen. The lateral face of the ramus is plane, except as it flares laterad forming a prominent capsule of the incisor; the latter is strongly set off from the ascending ramus by a prominent groove. The ascending ramus lies in the same plane as the side of the jaw and originates at the level of the posterior margin of M_2 . Antero-posteriorly the basal margin of the jaw is shallowly convex; there is, however, a concave recurvature to the angular process at about the level of M_3 . The angle of the jaw appears to be slightly inflected. The remainder of the posterior portion of the ramus is lacking.

I₁ is somewhat more procumbent than in *Cupidininus*, but less so than in *Mookomys* Wood. In cross section, the tooth is relatively broader than in the latter genus and is more nearly equivalent to the former or to *Perognathus* Wied-Nieuwied.

The structure of P₁ is quite variable. It is seen to consist of four transversely ovate cusps; the anterior pair is not quite parallel with the hypolophid, since the metaconid is placed well anterior to the protoconid. The anterior borders of the protoconid and metaconid are closely connected by buttress-like tranverse extensions (Plate 1b). The molariform teeth are rather low-crowned (Figure 2) and become bilophodont very rapidly with wear. The hypolophid of P₄ loses its cuspularity much earlier than does the metalophid. The hypoconid bears an acuspulate shoulder-like lateral expansion. This structure is seen similarly in Mookomys altifluminis Wood. First union of lophs takes place between the protoconid and the hypoconid since the transverse valley rapidly deepens lingual to this point. Connection of the exposed dentine on the occlusal surface of the two lophs will thus, in all probability, first occur somewhat buccal to the center of the tooth.

 $\rm M_1$ and $\rm M_2$ are nearly identical except for a lesser anteroposterior length of the latter (Table 1). In both teeth the protoconid and metaconid are transversely ovate and are connected by extensions of their anterior borders. From this point a cingulum, as high as the apices of the cusps, curves laterad to the small, abliquely-elongate, protostylid. In $\rm M_1$ the protostylid extends slightly into the transverse valley (Plate 1b,) while in $\rm M_2$ the metalophid is nearly straight. In both teeth, when unworm, the cingulum extends briefly lingual from the junction of protoconid and metaconid.

The hypoconid is the longest and most prominent cusp of the posterior lophid; in M_1 it is set somewhat anterior to the other two cusps, thus displacing the transverse valley anteriad

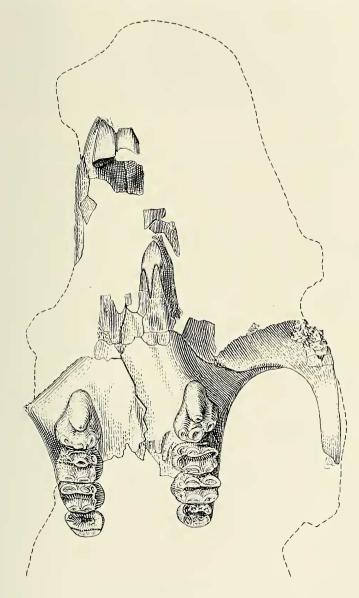


PLATE 40

Trogomys rupinimenthae new genus and species; holotype, LACM (CIT) 5184, palate and dentition.

near the center of the tooth. On M_1 , a rather distinct posterior cingulum connects the entoconid, the posterior surface of the hypoconid, and the hypostylid. First junction of lophids occurs between the protoconid and hypoconid with a second high point of the transverse valley between the stylids. An ephemeral stage may occur in which enamel of the transverse valley is completely surrounded by dentine, but is not evidenced in the little-worn specimens at hand. With moderate wear, cuspularity of the lophids is highly reduced.

 $\rm M_3$ is similar in pattern to the anterior molars and appears to be sextituberculate. The protostylid is of relatively reduced importance and tends to penetrate posteriad into the transverse valley. The hypostylid is very much reduced and is closely appressed to the hypoconid, as in the other molars.

The holotype consists of a fragmentary anterior portion of the cranium and a partial brain cast. The referred specimen LACM (CIT) 5185 does not add appreciably to our information since the same parts of the skull are present; the dorsal skull surface is, at present, unknown. The palate is nearly flat from the anterior border of M¹ forward at least to the incisive foramina. A faint median keel is present at least between P⁴ and probably extends forward from this position. The incisive foramina, lying about 2.0 mm. anterior to P⁴, though not complete anteriorly, are seen to be rather wide, with nearly parallel lateral borders. The premaxillary-maxillary suture seems to cross the foramina at or near their posterior borders.

In this specimen the rostrum is distorted and the diastemal surface is almost completely absent. A marked concave curvature is evidenced, however, as the diastema decurves to the alveoli of the incisors. The entire rostrum appears to have been rather narrow, as in *Perognathus*; the planes of the lateral rostral surfaces are nearly parallel. The specimens are too badly eroded to give evidence as to the natural position of the infraorbital foramen. The entire curvature of the upper incisor is observable; the distance between the lateral surfaces of the incisors on the skull dorsum is about 2.2 mm. There is no evidence that the nasals had been tubular.

The zygomasseteric plate lies in a plane nearly perpendicular to the sagittal plane of the animal and rises sharply dorso-laterad from the palate, as in most species of recent *Perognathus* examined. Curving postero-ventrad, the zygomatic process is rapidly reduced in breadth. The ventral edge of the plate and



PLATE 41

Trogomys rupinimenthae new genus and species; referred specimen LACM (CIT) 5190, left ramus and dentition.

the zygomatic process describe a symmetrical concavity. It thus appears that the lateral borders of the zygomatic arches were not parallel, but rather were slightly flaring and laterally convex. The dorsal surface of the zygomatic process is not expanded in breadth to the extent seen in *Cupidinimus* but rather is again reminiscent of the structure of *Perognathus*.

The dorsal bones of the rostrum and cranial vault are largely lost in the available materials. The general shape of the right orbital region appears to approximate that of *Perognathus*. A supra-orbital ridge of the frontal is present at the least interorbital constriction. Including the breadth of this lateral overhang, the least interorbital distance seems to have been about 4.0 mm. Since there is some doubt as to the extent of development of this supraorbital ridge, the above measurement is likely to be an underestimate of the true value.

As is expected, the brain cast exhibits a central longitudinal sulcus; at the rear of the orbit, the brain flares laterad to the cerebral hemispheres. There is no definitely discernible posterior margin of the cerebrum or lines showing the presence of overlying sutures. A facet on the posterior third of the dorsolateral interorbital surface may be indicative of the extension of the squamosal onto the skull dorsum. There is no direct evidence as to the size of bullae, since it is impossible to say with certainty whether the rounded bulla-like bulge of matrix on the right ventral surface has been artificially formed and worn, or whether it is a true bullar cast.

I¹ is asulcate, no indication of a groove being seen. On the occlusal surface of the upper incisor, specimens consistently show a medial groove resulting from deep attrition of the narrow lower incisors. There was evidently little or no lateral movement in biting with the incisors since the grooves are exactly the width of the two appressed lower incisors.

The molariform teeth lie in parallel rows with an interalveolar distance of about 2.0 mm. The teeth do not exsert perpendicular to the palatal plane, but rather diverge slightly latero-ventrad. The teeth are brachydont (Figure 1) though not to the extent observed in Mookomys formicorum Wood. There is no approach to the advancing hypsodonty of Cupidinimus. The molariform teeth are little reduced from front to rear (Table 1). P4 and M1 are about equal in width. M2 is about 5 per cent narrower than M^1 , while M^3 is about 75% of width of M^1 . This reduction is less than that observed in most Recent Perognathus and is more nearly similar to that of Cupidinimus. P4 (Plate 1a) is formed of a slender, elongate protocone which lies directly anterior and most closely connected to the transversely-ovate hypocone. The metaloph is crescentic with the ovate metacone lying anterior to the other cusps and joined fully with the hypocone. Medially the antero-posteriorly elliptical hypostyle is nearly connected by a cingulum to the hypocone, being separated therefrom only by a sulcus cutting rather deeply between them. The first junction of lophs with wear occurs between the protocone and the hypocone.

The molars are sextituberculate and vary but slightly in structure. Though lophodont, the cuspal patterns are clearly evident and are moderately persistent.

As is to be expected, the protocone is set between and behind the paracone and protostyle; these latter are connected anteriorly to the protocone by a prominent cingulum. The protostyle lies closer to the protocone than is the latter to the paracone. The metaloph consists of the metacone and hypocone, transversely oriented and closely connected, with the hypostyle placed slightly anterior to the line of the other two and closely joined to the hyprocone. Medially, the protostyle and hypostyle are joined nearly to their apices, thus effecting a closure of the transverse valley.

 M^2 varies from M^1 in its lesser antero-posterior dimension (Table 1). The protocone is less displaced posteriorly and the anterior cingulum is much less distant. M^3 is sexticuspulate; the styles are joined medially as in M^1 and M^2 . Wear has broadened the metaloph of M_3 to a wide surface. Connection of the paracone and metacone buccally thus completes the enamel ridge surrounding the deep pit-like transverse valley which persists as a central pit for nearly the life of the tooth.

_	
e	
_	
ð	
ľa	

M3	им АР	0.75	0.78	02.0	0.72		M3	мн АР	0.72 0.77	*0.77 *0.80	*0.75 *0.68	0.83 *0.80	0.80	Trogomys rupnimenthae new genus and species, measurements of upper and lower teeth. Abbreviations
7	WP	*0.92	0,95	1,05	1.03		~	WM W	0.88	06.0	0,95 *(0.97	- 86.0	eeth. Ab
	AP	0.83	0.82	0.83	1			ΑÞ	ł	0,93	0,85	0.92	0.87	Trogomys rupinimenthae new genus and species; measurements of upper and lower tee
<u></u> 21	WM	1.12	1,13	1,13	1,13		¥21	WH	1	1.00	1.08	1,18 1,15	1.20 1.12	and
	WP	1.18	1.18	1,22	1,23			WM	1	1,12	1.17	1.18	1.20	ipper
	AP	0.88	0.95	!	0.00			AP	ł	ł	1,03	1.02	1.02	of 1
٤i	WM	1.27	1	ł	1,30		M1	WH	1	1	*1,15	*1.17 1.02	*1.18	ement
	WP	ł	1.27	ŀ	1.37			WM	1	ł	*1,17	*1,18	*1,23 *1,18 1,02	measm
	AP	*1,30	*1.40	ł	1			AP	1,18	1.00	0.92	0.87	*0.82	species;
P4	MM	1,27	1,27	;	1	•	P4	WH	06.0	0.93	26.0	1	1	s and s
	WP	1	1	ł	1			WM	0.77	0.87	0.78	1	ł	nueg /
11	WP	0,63 1,05	1	1.02	;		11	AP	1.05	1.07	1	1	1	ae nev
H	P. C.		09.0	0.50	!		1	Æ	0.47	0.47	ł	1	ł	imenth
		LACM (CIT) 5184-Rt.	LACM (CIT) 5184-Lt.	LACM (CIT) 5185-Rt.	LACM (CIT) 5185-Lt.				5188	5190	5186	.87	89	s rupin
		CIT) 51	CIT) 51	CIT) 51	CIT) 51						CIT) 51	LACM (CIT) 5187	LACM (CIT) 5189	ogomy.
		LACM (LACM (LACM (LACM (LACM (CIT)	LACM (CIT)	LACM (CIT)	LACM (LACM (Tr

Relationships: It is suggested that the three genera *Perogna*thus, Mookomus, and Trogomus are closely related and may be united as the subfamily Perognathinae. The three included gepera are united by molar characteristics of moderate lophodonty with concomitant low crown. In characteristics of the ramus and cranium the genus Trogomys is quite similar to Perognathus. It differs, however, in lacking sulci on the upper incisors; this groove is present in *Perognathus* and apparently as well in *Moo*komys. Depending on one's preconceptions, since firm evidence is absent, the lack of incisoral groove could be primitive and retained through time as a separate line or it could have resulted from secondary loss of a previously present sulcus. In addition the molariform teeth of *Trogomys* possess strong cingula, which appears to be a primitive characteristic which has persisted. It is therefore the present contention that Trogomys, retaining these features of older heteromyid forms, represents a distinct line continuing into Tick Canyon time but which presumably had a rather long previous separate history.

Nothing is known as to the path by which the derivative perognathines descended from ancestral forms. Wood has supported *Heliscomys* as the ancestral genus. While agreeing that the latter genus is old, it is, nonetheless, specialized to an extent which suggests it to be removed, to some degree at least, from the stem of perognathine divergence. The other known Oligocene forms include the genus *Proheteromys* (sensu latissimo) of Wood and two new genera of heliscomyine structure (Reeder, 1960). Though no known specimen of the early *Proheteromys* group is as small as *Trogomys*, *Mookomys*, or most *Perognathus*, it appears that these specimens represent a more generalized structural stage which could have given rise to the perognathine dental type. Detailed discussion of Wood's genus *Proheteromys* will be found elsewhere (Reeder, 1956).

The presence of this new perognathine in the Tick Canyon formation at present can contribute little to the accurate dating of the formation. The obvious primitive nature of the remains, however, would suggest late early Miocene or early middle Miocene time of deposition to be reasonable and not out of line with the evidence presented by Jahns (*op. cit.* pp. 169-173) and Dawson 1958.

Environment: Two large fossil floras and several smaller ones have presented evidence which bears on the determination of physical and floristic conditions under which the Tick Canyon sediments were deposited. The Tehachapi flora, nearly contemporary with Tick Canyon, was deposited on the western margin

of Mohavia near the present town of Tehachapi (Axelrod, 1939). The Upper Miocene Mint Canyon flora (Axelrod, 1940) followed the Tick Canyon formation considerably in time, but occurs in the same stratigraphic sequence, documenting a more recent floral community, but of the area from which Trogomus derived. Axelrod (1950) has suggested that in the western region now desert, during Miocene time, the "Madro-Tertiary Flora, with its live oak woodland, chaparral, and arid subtropical scrub vegetation, characterized the regions of the present Mohave and Sonoran Deserts" (op. cit. p. 286). The climatic trend to increasing aridity, which continued into the Pliocene, shows continued restriction of lowland forest and woodland, with replacement by grass- and shrub-land. In a more recent summary, Axelrod states that "The Madro-Tertiary Geoflora was already the dominant vegetation in southeastern California by Early Miocene time . . . The absence of humid subtropical to warm temperate relicts in the Early Miocene of southeastern California suggests that the geoflora may have already been well established there by the Middle Oligocene, and possibly by Middle Eocene time" (Axelrod, 1958, p. 463).

Deposition of the Tick Canvon fauna occurred in deep lake waters surrounded largely by vegetation of arid or semi-arid facies. A riparian community, including hackberry, sycamore, and sabal palm, characterized the stream-border habitats and perhaps also the margins of the lakes. An arid subtropic scrub probbly grew on lower slopes surrounding the lake basins; this "plant formation was common along the river valleys and drier plains of interior southern California from Early Miocene (or earlier) well into Middle Pliocene time" (op. cit. p. 502). Reasoning from the Tehachapi conditions, the higher dry slopes probably were characterized by live oak savanna and scattered chaparral. The Tick Canyon fauna thus probably lived under temperature conditions similar to those now prevalent in the region, with the exception that winter temperatures were somewhat higher than at the present time. Rainfall varied from 15 to 25 inches annually, with biseasonal distribution as summer showers and winter rains.

It may be postulated that the absence of *Trogomys* from previously-known fossil assemblages is due to 1) the semi-arid nature of its habitat and the concomitant improbability of its preservation, or 2) its recent migration, in company with elements of

the north Mexican flora, from areas to the southeast which are biotically very little known in the lower and middle Tertiary. It is suggested that the geographic region within which the Madro-Tertiary Geoflora probably evolved, (the border-tropics of north-western Mexico and adjacent parts of southwestern United States) was simultaneously an area in which mammals also were changing, better to adapt to the developing arid conditions.

LITERATURE CITED

Axelrod, D. I.

- 1939. A Miocene flora from the western border of the Mohave Desert. Carnegie Inst. Wash., Pub. 516; 1-129.
- 1940. The Mint Canyon flora of Southern California: a preliminary statement. Amer. our. Sci., 238: 577-585.
- 1950. Evolution of desert vegetation in Western North America. Carnegie Inst. Wash., Pub. 590: 215-360.
- 1958. Evolution of the Madro-Tertiary Geoffora. Botanical Rev. 24: 433-509.

Dawson, M. R.

1958. Later Tertiary Leporidae of North America. Univ. Kansas Paleont. Contrib., Vertebrata, art. 6, pp. 1-75.

Jahns, R. H.

1940. Stratigraphy of the easternmost Ventura Basin, California, with a description of a new lower Miocene mammalian fauna from the Tick Canyon formation. Carnegie Inst. Wash. Publ. 514, pp. 145-194.

Reeder, W. G.

- 1956. A review of Tertiary rodents of the family Heteromyidae, Thesis, Univ. Michigan, pp. I-XXIII, 1-618, microfilm.
- 1960. Two new rodent genera from the Oligocene White River formation (Family Heteramyidae). Fieldiana (Geology), 10:511-524.

Wood, A. E.

1935. Evolution and relationship of the heteromyid rodents with new forms from the Tertiary of Western North America. Ann. Carnegie Mus., 24: 73-262.